Final Report

JVA 01-JV-112222048-150

Whitebark Pine Regeneration After Fire: Effect of Rust Mortality on Nutcracker Seed Dispersal

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This final report is based on "Evaluating Natural Selection as a Management Strategy for Restoring Whitebark Pine," a thesis by Shawn T. McKinney, directed by Diana F. Tomback, and submitted to the Department of Biology at the University of Colorado at Denver in partial fulfillment of a Master's degree, spring 2004.

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Introduction

Whitebark pine (*Pinus albicaulis* Engelm.), a keystone species of subalpine forests in northwestern United States and southwestern Canada, is in danger of regional extinction (Arno 1986, Tomback et al. 2001). Decades of fire suppression and an introduced fungus, white pine blister rust (WPBR) (*Cronartium ribicola*) have acted to reduce whitebark pine regeneration for about the last seventy years. One proposed management solution – the natural selection stand approach– predicts that observed levels of genetic resistance to WPBR, coupled with silviculture treatments that reduce site competition and increase seed caching opportunities for Clark's nutcracker (*Nucifraga columbiana*), will lead to stands dominated by rust-resistant trees (Hoff et al. 1994). However, little is known about the ecological effect of WPBR on pre-dispersal survival of seeds, and therefore, the likely success of this strategy.

Ovulate cones of whitebark pine are indehiscent at maturity and are produced in the upper third of the crown (Mirov 1967; McCaughey and Schmidt 1990). Whitebark pine is functionally an obligate mutualist because it requires the Clark's nutcracker to disperse its large and wingless seeds (Tomback and Linhart 1990). The nutcracker is a facultative mutualist since it relies upon nutritious whitebark pine seeds but also utilizes other sources of food, such as small vertebrates, carrion, insects, vegetable matter, and seeds of other *Pinus* species (Tomback and Linhart 1990; Guintoli and Mewaldt 1978; Tomback 1978).

When whitebark pine seed coats harden (as early as August 15), nutcrackers break into cones, gather seeds in their sublingual pouch, fly to a cache site, and deposit them in the substrate (Tomback 1978). Nutcrackers cache seeds in a variety of locations, but tend to cache seeds in recently disturbed open areas such as those created by fire (e.g., Tomback 1986). By dispersing whitebark pine seeds into recently burned areas, nutcrackers are

responsible for the early successional status of the species (Tomback 1982; Tomback and Linhart 1990).

Prior to seed coat hardening, however, nutcrackers break into whitebark pine cones and consume unripe seeds. This can occur as early as mid-July (Tomback 1978). During this period (mid-July to mid-August), the nutcracker is a seed predator that reduces the seed crop .

Nutcrackers are not the only threat to a stand's seed crop. Red squirrels (*Tamiasciurus hudsonicus*) are known to deplete the seeds available for avian dispersal (Benkman et al. 1984; Benkman 1995; Samano and Tomback 2003). Benkman et al. (1984) found that 80 percent of the seed cones of limber pine (*Pinus flexilis* James) (a bird-dispersed pine) were harvested by red squirrels prior to opening. These results were contrasted with forests where squirrels were absent, and only 30 percent of the cones were lost prior to time of dispersal. The loss of seeds to red squirrels can be so great that it alters energy allocation within a population of pines. Benkman (1995) reported that limber pine allocated more than twice as much energy to seeds in the absence of squirrels compared to areas where they were present.

Whitebark Pine Decline

Whitebark pine is declining throughout much of its range for two main reasons: fire suppression and white pine blister rust. In the Northern Rocky Mountains, whitebark pine is a successional species on favorable sites and relies upon periodic fire to reduce encroachment by its competitors, primarily Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) and subalpine fir (*Abies lasiocarpa* Hook.) (Arno and Hoff 1990; Arno 2001). The successful exclusion of fire from the landscape since around 1929 has altered this process and created conditions unfavorable for whitebark pine. Also, fire suppression has reduced

the number of openings in the forest suitable for nutcracker caching and whitebark pine seedling growth, which has further exacerbated successional replacement (Keane et al. 1994).

The second leading cause of whitebark pine decline is white pine blister rust. Cankers caused by the rust form on a tree, first killing the branches, then the crown, and eventually the entire tree (McDonald and Hoff 2001). Most importantly, because seed cones of whitebark pine form in the upper crown, cone production ceases and an infected individual becomes reproductively dead well before the tree itself dies (Arno and Hoff 1990).

Mortality induced by blister rust infection is as high as 90 percent in some stands in regions such as the northwestern Rocky Mountains and the Olympic and Cascade ranges (Kendall and Arno 1990; Keane et al. 1994). Throughout the northwestern United States and southwestern Canada, WPBR infection levels range from 20 percent to 100 percent (Kendall and Keane 2001). Blister rust is spreading geographically within the range of whitebark pine and intensifying within stands (e.g., Campbell and Antos 2000; Zeglen 2002). It has the potential to result in regional extirpation of the species.

Keane et al. (1996) compared the historical distribution of whitebark pine in the interior Columbia River Basin and Bob Marshall Wilderness Complex in Montana to its current range and estimated that it has declined by 45 percent during the past 100 years. Further evidence of population decline also comes from the Bob Marshall Wilderness Complex where fewer than 10 percent of whitebark pine stands sampled had any regeneration younger than fifty years old (Keane et al. 1994).

Within heavily infected stands, however, researchers rarely observe 100 percent mortality from WPBR, and in some of these stands at least one to a few canker-free trees are identified. Such observations suggest resistance to WPBR. Field observations of phenotypically resistant trees were confirmed in the laboratory by Hoff et al. (1994) who

demonstrated that surviving whitebark pine trees from high-mortality stands possessed higher levels of heritable resistance than individuals from stands exhibiting lower mortality. In addition, more than 40 percent of progeny grown from seeds collected from healthy survivors of heavily impacted stands demonstrated some resistance to the rust (Hoff et al. 2001).

Problem Statement

The natural selection stand approach to whitebark pine management was proposed to ameliorate the conditions wrought by blister rust and fire exclusion by utilizing processes occurring on the landscape – natural selection favoring rust resistant trees and seed dispersal by nutcrackers. The proposal maintained that if areas adjacent to stands that contained at least a few rust-resistant trees were cleared of vegetation, nutcracker caching opportunities would be created and site competition would be reduced. In about 50 years, a new stand dominated by rust-resistant whitebark pine would exist (Hoff et al. 1994).

This approach would be an attractive management solution that is low in cost and labor if it were not for the possible effect of seed predators on an inherently diminished cone crop. High mortality areas have low whitebark pine tree density and likely low cone density. If there is not a corresponding reduction in the number of seed predators in the area, the seed predator to cone density ratio will greatly increase. Such a change in this relationship could result in a depletion of the cone crop before mid-August when nutcrackers begin to disperse seeds.

Therefore, does WPBR reduce whitebark pine cone density, and if so, does a decrease in density lead to lower pre-dispersal survivorship of whitebark pine seeds? This study examined the influence of WPBR on cone density, pre-dispersal seed survival, and the

likelihood of seed dispersal across similar stands that varied in degree of WPBR infection, crown kill, and mortality. We postulated that: (1) stands with higher levels of WPBR will have lower cone densities than similar stands with lower rust levels, (2) stands with lower cone densities will have a smaller proportion of their cones survive to time of seed dispersal, and (3) stands with a lower proportion of cones surviving will be less likely to have seeds dispersed by nutcrackers.

Methods

Study Sites

Field sampling was conducted from 15 July to 4 September 2001 and from 15 July to 10 October 2002 in west-central Montana and east-central Idaho. Study sites were selected based on the distribution of whitebark pine and known levels of WPBR infection. Within each study site, two stands were selected for detailed observation. Stands were selected based on their accessibility, distance from established cone collection sites, and density of cone-bearing whitebark pine trees.

Blister rust infection levels are high in the Bitterroot National Forest, Montana, and the Saddle Mountain study site was selected to represent that condition. The higher elevation stand within this site was dominated by whitebark pine. This stand, Saddle Mountain Upper, was located on the side of Saddle Mountain (45°43'N, 114°59'W, 2574 m elevation). The lower elevation stand at this site was comprised of a mixed association of species, and whitebark pine was successional. This stand is referred to as Saddle Mountain

Lower (45°41'N, 113°58'W, 2451 m elevation). Both stands were adjacent to areas burned by wildfire in 2000.

The site containing lower blister rust infection values was located within the Salmon National Forest, Idaho, and is referred to here as Blue Nose study site. Within this site, the higher elevation stand was characterized as whitebark pine climax and is located on Blue Nose peak. This stand is referred to as Blue Nose Upper (45°28'N, 114°21'W, 2660 m elevation). The lower mixed association stand is referred to as Blue Nose Lower (45°27'N, 114°20'W, 2553 m elevation). All four stands sampled in this study were approximately one hectare (ca. 100 x 100 m) in area and were accessible by a short walk from established roads.

Within each stand, all trees > 1.5 m in height and > 1 cm diameter at 1.3 m above the ground (diameter at breast height DBH) were measured for height and DBH. All individuals < 1.5 m in height or < one cm DBH were tallied and recorded by species.

All whitebark pine trees within each stand were inspected for the presence of blister rust and tree damage from rust. A tree was considered to have the rust if it exhibited active and inactive branch or bole cankers, branch or bole blisters, and/or a dead or partially dead crown. We estimated the percentage of crown kill for all whitebark pine trees that showed symptoms of the rust. Percentage crown kill is a categorical variable used to estimate the relative damage to a tree's crown. The crown of a tree was considered to include the area from the highest point of the tree down to the lowest branches. Dead whitebark pine trees were tallied and, if possible, their cause of death determined. The higher the percentage of blister rust-infected trees, the greater the average crown kill, and the greater the percentage of dead trees, the more severe the blister rust infection in the stand.

Methods and Materials

All whitebark pine trees with seed cones were counted and tagged with a specific identification code. A tree's identification code was used for all other data or measurements obtained for that individual. Densities of cone trees in the different study stands were similar (mean=29.2/ha, min=27, max=32).

In mid July of 2001 and 2002, we counted all seed cones present on these trees. This value is referred to as the initial number of cones and is used to calculate stand means, and initial cone density per tree. A spotting scope with a 1x ocular and 40x objective, and 8 x 32 binoculars were used to survey and count cones. Cones were tallied with a handheld counting device. This procedure was repeated between 10 and 16 days apart for all cone-bearing trees within all stands.

The time of seed dispersal was determined for each stand when at least one nutcracker was observed pouching seeds from a whitebark pine tree in the immediate area. Following such an observation, we conducted another cone count in the stand. The value obtained from this count is referred to as the final number of cones. Therefore, we observed nutcrackers pouching in each study site before conducting a final cone count in the study there.

Pine seed predators that frequented these stands consisted primarily of Clark's nutcrackers, red squirrels, and to a lesser extent, chipmunks (*Tamias* spp). Stands were monitored for animal activity between 0530-2030 (minimum=two hrs. maximum=eight hrs.) throughout the summer (mid-July to September). Field data were converted into the number of sightings per hour for each predator. Observation periods were distributed evenly within this timeframe to reduce temporal variation in animal activity. During observation periods, time was split between surveying from vantage points with spotting

scope and binoculars or by moving throughout the stand. Observations of squirrels and chipmunks were divided into two categories: 1) seed/cone harvesting or 2) presence in the stand but not harvesting. Nutcrackers observations were separated into three categories: 1) seed harvesting 2) seed pouching or 3) within stand but not on cones.

The overall seed predator rate (SP) for each stand was calculated by the following:

$$SP = (ClNu + ReSq + Chip) * 1000$$

ClNu = total of nutcracker seed harvesting observations/total hours of observation

ReSq = total of red squirrel seed or cone harvesting observations/total hours of observation

Chip = total of chipmunk seed harvesting observations/total hours of observation

Data Analyses

Data were plotted and tested for normality by looking at median, mode, and mean values, histograms, and values of kurtosis and skewness. Descriptive statistics were calculated for cone counts, blister rust infection levels, whitebark pine trees, and basal area data. Levine's test was used to test the null hypothesis of homogeneity of error variance for cone data (initial and final number).

Data from 117 whitebark pine trees that produced 2,008 cones were analyzed. Cone survival was determined by analyzing the relationship between the number of final cones and the number of initial cones for all trees in each stand by linear regression. A spreadsheet was used to create a table of basic comparisons in regression for all cone data. With these results, we calculated an F-test for homogeneity of slopes of the four regression lines (four stands) in order to test the null hypothesis that seed survival is equal across all stands. We used the Tukey-Kramer Procedure (Dunnett 1980) to calculate minimum significant differences between pairs of regression coefficients (b) with 95 percent confidence. Gabriel's

Approximate Method (Gabriel 1978) was used to calculate 95 percent comparison intervals among all *b*'s to determine specifically which stands were significantly different, in terms of *b*, from one another.

The proportion of cones surviving to time-of-caching by nutcrackers was calculated as follows: no. of final cones/no. of initial cones. This value was determined for each whitebark pine cone tree and as stand means. The mean proportion surviving was regressed against the ratio of seed predators to initial cone density for all stands to test the strength of the relationship of predator abundance and initial cone density with cone survival. The proportions of cones surviving to time of dispersal were also compared with the severity of blister rust infection and tree damage within study stands-- i.e. percent infected, percent crown kill, and percent mortality.

Results

Blister Rust Effects on Initial and Final Cone Density

Results indicated that high WPBR severity – as apparent from high levels of infection, crown kill, and mortality - was associated with a reduction in cone density. Blister rust infection levels and damage were greatest and cone density was lowest in the Saddle Mountain stands. The two low elevation stands, Blue Nose Lower and Saddle Mountain Lower, and high elevation stands Blue Nose Upper and Saddle Mountain Upper, were otherwise similar to one another in structure and whitebark pine attributes (Table 3.1).

The stands with lower cone densities did not have correspondingly fewer seed predators (number of sightings per hour). The absolute occurrence rates of seed predators failed to show a trend with increasing WPBR severity.. However, when the occurrence rates of seed predators were viewed in relation to initial cone density, a clear trend emerged: Aas

the WPBR damage and infection levels increased, the numbers of seed predators per cone also increased (Figure 3.1). Thus, the Saddle Mountain stands, where WPBR infection and damage were the greatest, had the highest occurrence rate of seed predators relative to the initial number of whitebark pine cones.

Table 3.1 Comparison of stand characteristics among four whitebark pine stands sampled in western MT and eastern ID. BN Lower and SM Lower were lower elevation successional whitebark pine stands. BN Upper and SM Upper were higher elevation climax whitebark pine stands. All stands were one hectare (100 x 100 m).

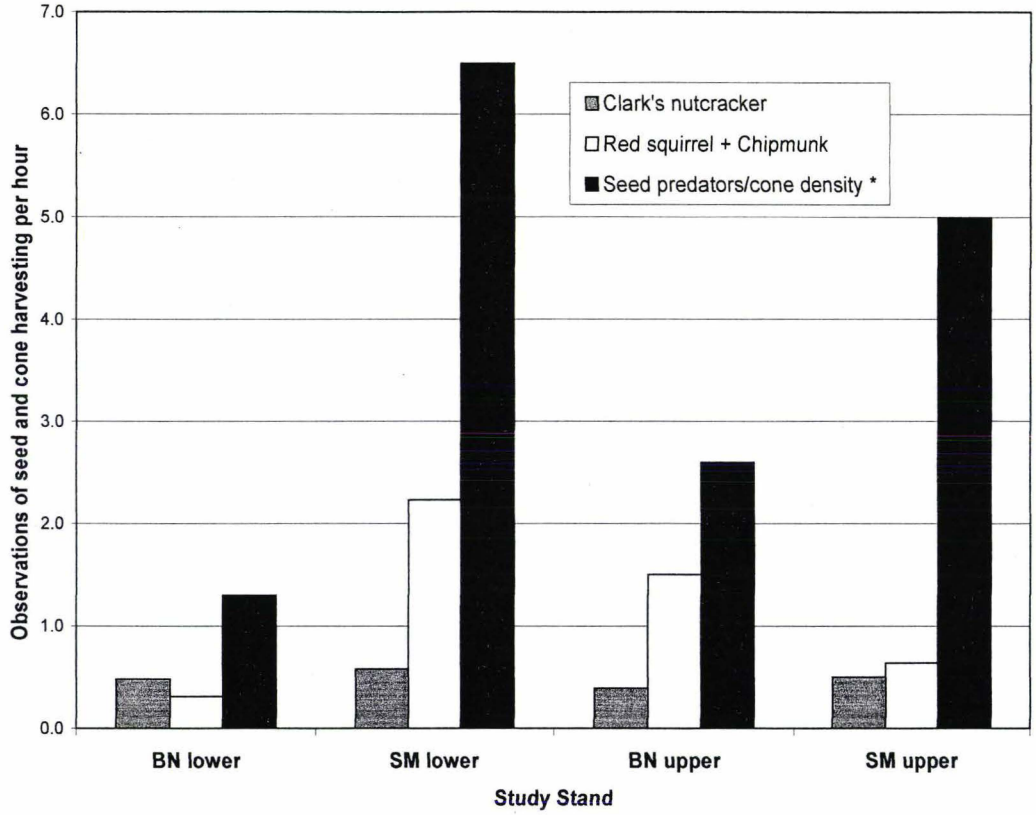
	Study Stand			
Variable	**BN Lower**	**SM Lower**	**BN Upper**	**SM Upper**
No. of cone trees	28	27	30	32
Cone density (No./ha)	624	432	723	227
Infected (%)[a]	24	97	54	96
Mean crown kill (%)[a]	3	79	13	38
Mortality (%)[a]	0	29	3	18
Mean DBH (cm)[b]	19	21	15	13
Mean Height (m)[b]	12	14	7	8
Total basal area (m^2)	3.5	5.4	2.1	2.3
Relative dominance (%)	45	45	91	96
Relative cover (%)	58	46	90	95

Note: Data are for whitebark pine trees only.

[a] White pine blister rust values for all whitebark pine trees in a stand.

[b] Cone-bearing trees only.

Figure 3.1 Differences in seed predator occurrence rates among four whitebark pine stands. Stands are paired with their ecological counterpart (BN lower with SM lower and BN upper with SM upper). The Saddle Mountain area had greater blister rust damage than the Blue Nose area.



Note: * Seed predator/cone density values are combined rates of nutcrackers, red squirrels, and chipmunks harvesting seeds or cones divided by the initial density of cones x 1000.

Cone Survival

Regression analyses of cone counts indicated a significant relationship between the initial number of cones (mid-July) and the number available at time of seed dispersal (mid-August) in the Blue Nose study stands, where blister rust infection and damage are low. At the Saddle Mountain study site, where blister rust is more severe, there was a weak but

significant relationship between initial and mid-August cone counts for the upper stand. However, the relationship was not statistically significant in the lower stand (Table 3.2).

An F-test comparing the regression coefficients of the four study stands revealed significant differences among their regression slopes ($F_{.05\,[3,68]}=2.75$) (Table 3.3). In the lower elevation stand at Blue Nose, where WPBR infection and damage were the lowest of all stands sampled, the slope of the regression line of the number of cones remaining at time of seed dispersal and the number present in mid July was significantly steeper than the slope for all the other stands. In addition, the slope of the regression line for Blue Nose Upper was significantly greater than the Saddle Mountain lower elevation stand but greater than the ecologically similar Saddle Mountain upper stand. The two Saddle Mountain stands did not differ significantly from each other in terms of cone survival (Figure 3.2).

Table 3.2 Linear regression analyses of the number of cones available at time of seed dispersal on the number in mid-July. SM Lower and SM Upper had greater damage from blister rust than their ecologically similar BN Lower and BN Upper.

	Study Stand			
Variable	**BN lower**	**SM lower**	**BN upper**	**SM upper**
b_i[a]	0.88	0.07	0.51	0.21
S_{bi}[b]	0.04	0.09	0.05	0.16
R^2	0.95	0.10	0.71	0.29
p	$4.1\ E^{-18}$	0.1	$3.8\ E^{-9}$	0.001

Note: p-values with * indicate statistical significance at $\alpha=0.05$.

[a]: Regression coefficient (slope of the regression line) for an individual stand.

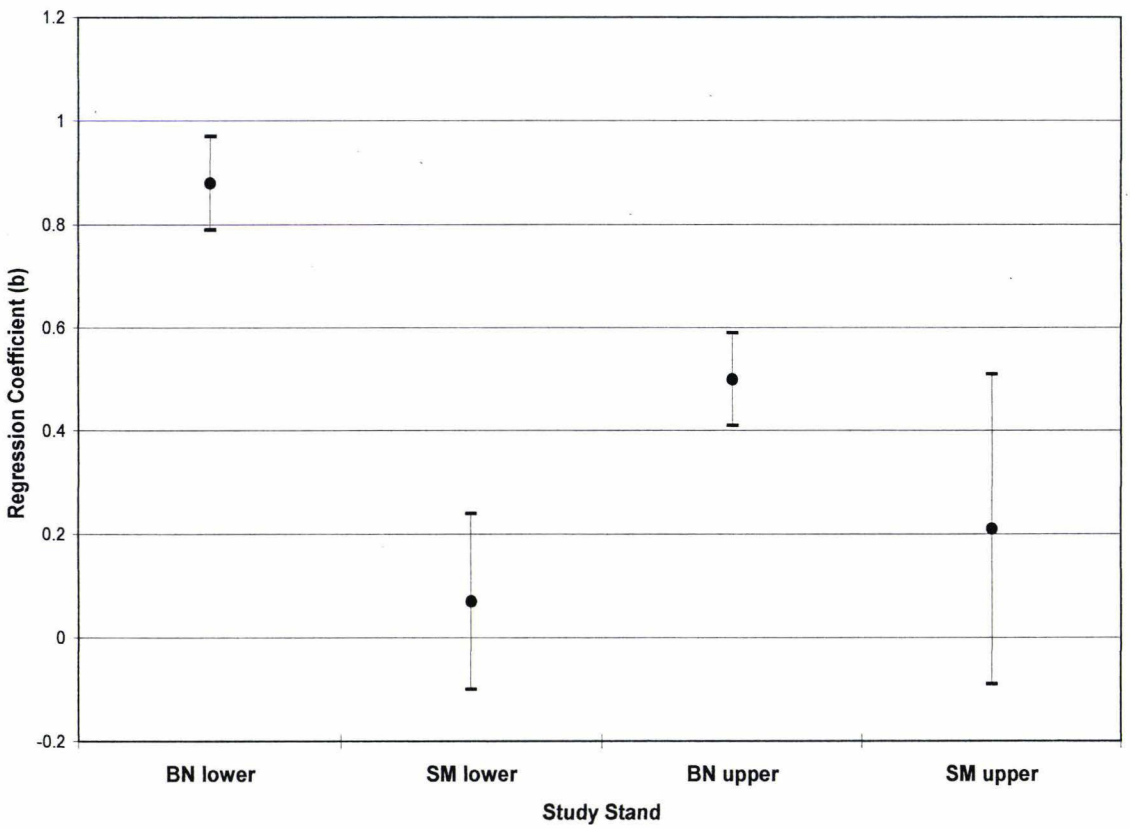
[b]: Standard error of the regression coefficient.

Table 3.3 F-test for equality of slopes of regression lines of cone survival. Four whitebark pine stands were sampled in western MT and eastern ID.

Sources of Variation	*df*	SS	MS	F_s
Among *b*'s (variation among regressions)	3	1120.6	373.5	8.68*
Weighted average of deviations from regression (average variation within regressions)	68	2920.7	42.9	

Note: * indicates that there were significant differences at $\alpha = 0.05$ among the four stands when testing for homogeneity of the regression line.

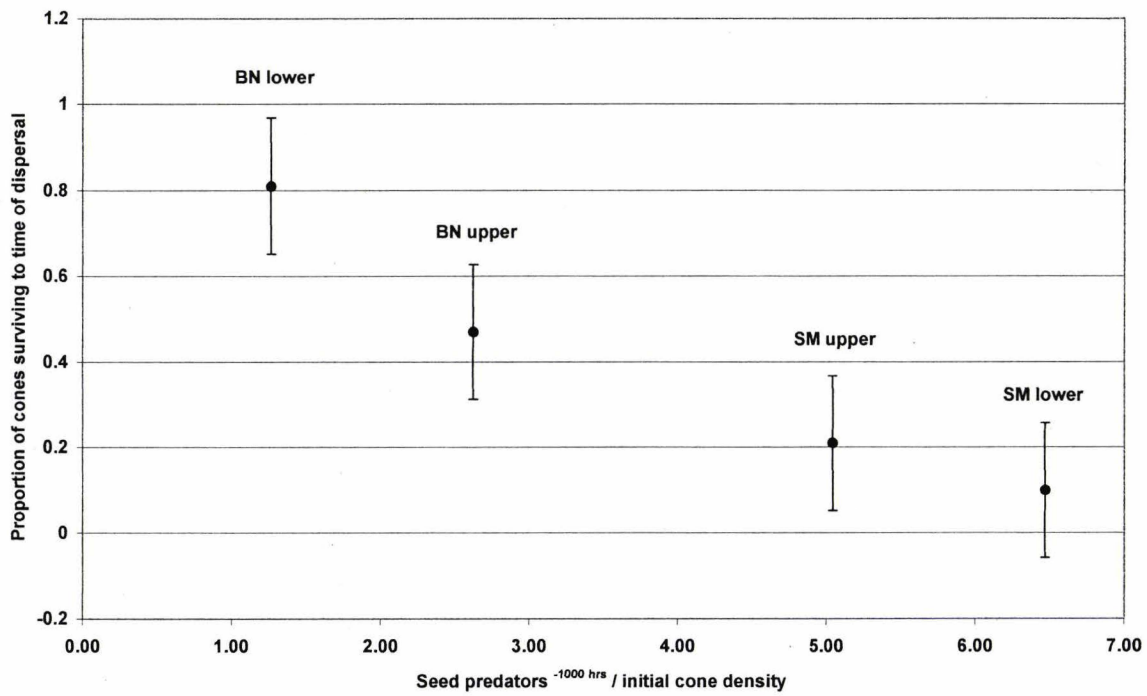
Figure 3.2 Comparison intervals for regression coefficients of the number of whitebark pine cones remaining at time of seed dispersal on the number of cones available in mid-July for the two Saddle Mountain study stands and two Blue Nose study stands. . Four stands from western MT and eastern ID were sampled. Two regression coefficients are significantly different at a five percent experiment-wise error rate if and only if their intervals do not overlap.



Note: Confidence intervals were calculated using Tukey-Kramer Procedure. Comparison intervals were plotted using Gabriel's Approximate Method. Middle points represent b, the regression coefficients of the samples, upper bars the upper limits, and lower bars the lower limits of the intervals with 95% confidence.

The ratio of seed predator occurrence rate to initial cone density had a significant and negative linear relationship with the proportion of cones surviving to time of seed dispersal ($R^2 = 0.95$, $p < 0.05$) (Figure 3.3). Overall, by study site, there were significantly more cones available for nutcrackers at time of seed dispersal at Blue Nose than at the Saddle Mountain site (single-factor ANOVA $F_{.05}$ [3,113] = 29.4, $p<0.05$). A higher proportion of cones surviving favored the likelihood of nutcrackers pouching and or caching seeds in a study stand (Table 3.4).

Figure 3.3 Relationship between the ratio of seed predators to cone density and the proportion of cones surviving to seed dispersal among four whitebark pine stands, Blue Nose Upper, Blue Nose Lower, Saddle Mountain Upper, and Saddle Mountain Lower..



Note: X axis values are the sum of observations of nutcrackers, red squirrels, and chipmunks harvesting seeds and cones per hour of observation times 1000, and divided by the density of cones in a stand. Bars represent standard error.

Table 3.4 Comparison of cone survival and observations of nutcrackers pouching and caching whitebark pine seeds. BN Lower and Upper had little damage from blister rust, SMLlower and Upper were more impacted by the rust.

	Study Stand			
Variable	**BN lower**	**SM lower**	**BN upper**	**SM upper**
Cone survival[a]	0.81	0.10	0.47	0.21
Pouching[b]	0.41	0.07	0.36	0
Caching[c]	yes	no*	yes	no*

[a]: Proportion of cones surviving to time of seed dispersal by nutcrackers relative to the initial mid-July number.
[b]: Observations of nutcrackers pouching whitebark pine seeds per hour of observation.
[c]: Whether or not nutcrackers were observed caching seeds in a study stand. * indicates seed caching observed in study site area, but not within study stand.

Discussion

The likelihood of whitebark pine seed dispersal by Clark's nutcrackers varied greatly among the four one-hectare forest stands in western Montana and eastern Idaho. This can be explained by differences in stand conditions resulting from infection, tree damage, and mortality from white pine blister rust and other factors.

WPBR infection of whitebark pine acts to reduce cone density within a stand by killing cone-bearing branches and mature trees. Stands with higher degrees of infection, crown kill, and mortality had fewer cones/ha, fewer cones/tree in mid-July, and fewer cones/tree at time of seed dispersal in mid-August, relative to similar stands that had lower infection levels and damage by blister rust (Table 3.1).

Reduced cone densities of whitebark pine in high infection stands did not influence the frequency of seed predator observations. Populations of forest seed predators may be

experiencing a lag-time effect (i.e., not declining immediately) in terms of declining whitebark pine populations, or they may be sustained by alternative food sources such as the seeds of other conifers. Whatever the reason, it is clear that when the combined occurrence rates of seed predators were standardized to initial cone density, the number of seed predators was much greater in low cone density stands than in stands with higher densities (Figure 3.1).

Reduced cone density has significant effects on the number of cones available at time of seed dispersal (single-factor ANOVA $F_{.05}$ 3,113] = 29.4, $p<0.05$) and the relationship between the initial number (mid-July) and final number (mid-August) of cones (Figure 3.2). We found that in the low rust and high cone density stands at the Blue Nose site, the number of initial cones explained 95 and 71 percent, respectively for the upper and lower stand, of the variation in the number of cones left for seed dispersal. In contrast, with the high rust and low cone density conditions at Saddle Mountain, the initial cone number explained only 29 and 10 percent, for the upper and lower stand, respectively, of the variation in final cone number (Table 3.2).

When decreased cone densities are not met with corresponding reductions in seed predator occurrence, the proportion of cones surviving to seed dispersal decreases in a linear fashion (Figure 3.3). Within the Saddle Mountain stands, the cone densities were simply not high enough to withstand the pressure exerted upon the cone crops by nutcracker foraging and red squirrel harvesting. Mortality of cone-bearing branches -- whether by crown kill or tree death from blister rust or mountain pine beetle (*Dendroctonus ponderosae*) -- while unknot affecting seed predator densities, appears to be the most serious threat to cone survival in the whitebark pine stands studied. In other words, canopy kill reduces seed production, although predator densities are not affected.

Cone survival influences the likelihood of whitebark pine seed dispersal by Clark's nutcrackers. A lower proportion of cones surviving to time of dispersal means that there is a much lower probability of observing a nutcracker pouch and disperse seeds from a stand (Table 3.4). Therefore, the likelihood that a Clark' nutcracker will disperse seeds from a given area is negatively related to WPBR infection and damage at the stand level.

Implications to Management of Whitebark Pine

The natural selection stand approach to whitebark pine management relies upon the dispersal of rust-resistant seeds from stands heavily impacted by blister rust. However, we show that as damage from blister rust increases, the probability of seed dispersal decreases at the stand level. Therefore, stands with very high levels of mortality, damage, and infection (>80%) may rarely have seeds dispersed. These results suggest that we cannot assume that whitebark pine seeds from heavily impacted stands will be dispersed into areas prepared for restoration.

Factors influencing the pre-dispersal survival of whitebark pine seeds are more complex than this study addressed. Across the landscape matrix, there most likely will be areas with high and low values of cone survival that are not solely due to their levels of blister rust infection. Reduced cone densities from mountain pine beetle, fire, and logging activities will most likely lead to similar results.

A given stand's spatial relationship with other stands and conditions in the broader landscape will also undoubtedly influence cone survival. It is therefore imperative that during the site selection process of a restoration project, site-specific conditions are considered. Two potential seed source stands that are similar with regard to the presence of rust-resistant trees and in magnitude of cone density may be very different in terms of their

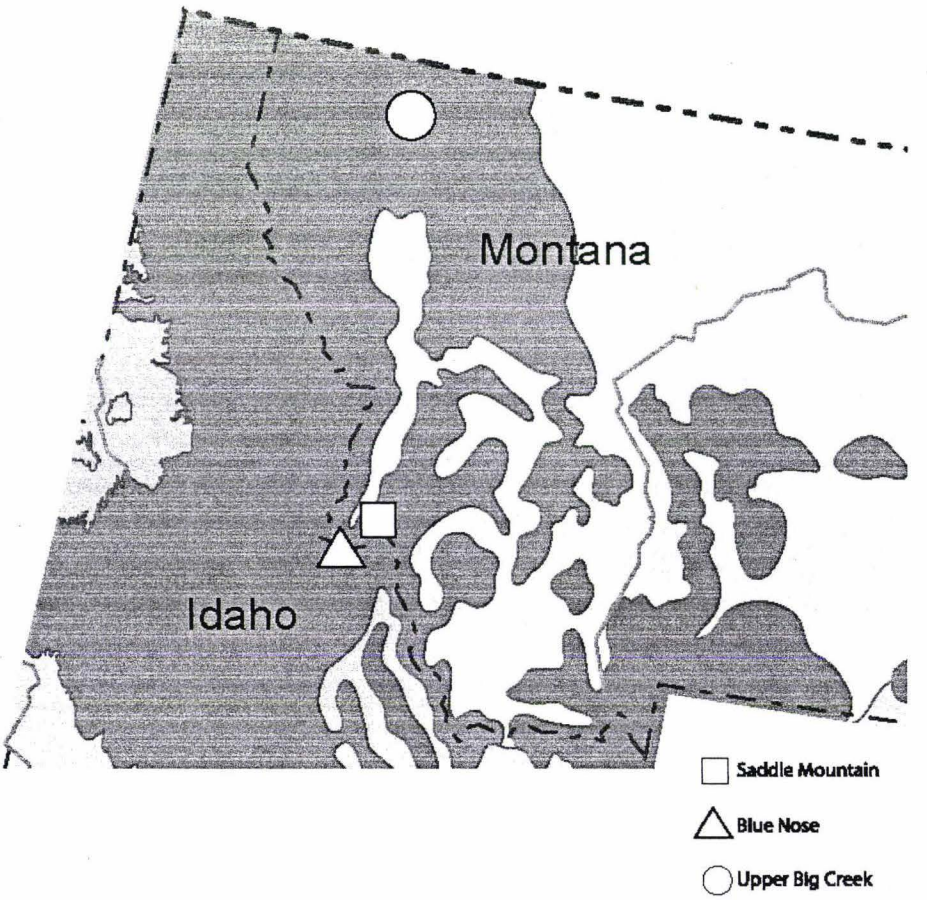
likelihood of cone survival based on their configuration and neighboring conditions on the landscape.

Cone survival, and thus the chance of seed dispersal from a given stand, will also vary with time. In the short term, the magnitude of the cone crop and, in the long-term, the effects of blister rust, pine beetle, and fire on the broader landscape, will most likely continue to shape the likelihood of seed dispersal and the chances of natural regeneration from a given area. Public land managers assigned the task of restoring whitebark pine habitat will have to consider both the characteristics of a seed source stand and its spatial relationship on the landscape in order to select the restoration approach that ensures the greatest chance for for success.

With white pine blister rust spreading and infection levels and mortality increasing in infected stands each year, the only way that whitebark pine will be maintained on the landscape in large portions of its range will be by hands-on restoration. Given the dynamics outlined in this paper, the natural selection stand model will probably not work under conditions typical of most heavily infected areas, arguing for more active intervention, such as burning or thinning stands in conjunction with planting rust-resistant seeds or seedlings. However, stands not as heavily damaged still have potential as natural seed sources. We are now challenged to take the next step to determine the various factors on multiple scales that affect the chance of seed dispersal from surviving stands.

APPENDIX

A. Map of western Montana and Idaho showing the spatial relationship of the three whitebark pine sites sampled from in this study.



B. Comparison Between 2001 and 2002.

In 2002, at the Saddle Mountain and Blue Nose study sites, the same 117 whitebark pine trees were surveyed that had been surveyed in 2001. Another small study stand, Saddle Mountain Ridge (31 m x 85 m) was also added that contained nine mature cone-bearing whitebark pine trees for a total of 126 trees surveyed in 2002. Only 318 seed cones were produced from these 126 trees compared to 2,008 cones produced by 117 trees in 2001. These results are indicative of a region wide low cone crop for whitebark pine in 2002.

There was a significant difference in the number of whitebark pine trees producing cones in the four study stands between 2001 and 2002 ($X^2_{calc} = 37.7$, d.f. = 3, $p < 0.05$). Consequently, in 2002, the initial and final numbers of cones were significantly reduced relative to 2001 (initial cone number $X^2_{calc} = 1{,}620$, d.f. = 3, $p < 0.05$, and final cone number $X^2_{calc} = 857$, d.f. = 3, $p < 0.05$).

An 84 percent reduction in the number of initial cones translated into a 94 percent decline in the number of cones available for nutcrackers at time of seed dispersal in 2002 compared to 2001. As a consequence, in the five stands monitored in 2002, we failed to observe nutcrackers pouch seeds in all of them except one, Blue Nose upper.

C. Upper Big Creek Study Site

Upper Big Creek study site was located within the Flathead National Forest, Montana. (48.31°N and 48.32°N and 114.23°W, 1696 m to 1805 m above sea level). This area consisted of a valley that was clearcut about thirty years prior to this study with the upper slopes and ridgeline that enclose the valley left unlogged. Located within this uncut area are many standing dead snags and fallen logs of once mature whitebark pine trees that have succumbed to WPBR disease and mountain pine beetle. Whitebark pine mortality in this area exceeds 80 percent. Within the opening adjacent to the uncut stands are many whitebark pine seedlings (< 1.5 m) and saplings (> 1.5 m). This site is one of the areas where Dr. Raymond Hoff observed phenotypically resistant mature whitebark pine trees and high densities of whitebark pine seedlings. We sampled at this site because it afforded an opportunity to directly evaluate the effectiveness of the natural selection stand hypothesis.

Due to high levels of mortality at Upper Big Creek, mature cone-bearing trees are rare and sparsely arranged on the landscape. Eleven cone-bearing whitebark pine trees along a five km transect were surveyed for cones. Height, DBH, degree of blister rust damage, and indication of seed predators were also recorded for these trees.

One important prediction that logically arises from the natural selection stand hypothesis is that the next generation of trees will show lower frequencies of WPBR. To tests this, on September 22, 2002, we surveyed two 50 m by 10 m transects that were approximately one km apart in the clearing adjacent to the whitebark pine stands. All whitebark pine seedlings and saplings were inspected for symptoms of the rust, and were measured for number of stems, heights, and diameters.

We sampled in the Upper Big Creek area in 2002 in order to test assumptions of the natural selection stand model. The first criterion of the model, that resistant trees will survive exposure to blister rust was supported. Five of the 11 cone trees surveyed showed no indication of blister rust, and of the six infected, the mean crown kill was only 16 percent. These trees were located in stands with mortality levels greater than 80 percent.

The second criterion of the model, that resistant individuals will have their seeds dispersed by nutcrackers failed to be supported. A 0.23 proportion of cones survived to time of seed dispersal among the 11 trees sampled, and we failed to observe nutcrackers pouching and dispersing seeds. These results indicate that this second condition had a low probability of realization in 2002.

Finally, we failed to confirm the presence of the condition for the third criterion; that resistance in the post-rust exposed generation will be higher in frequency than the pre-rust exposed generation. Results from the blister rust transects showed that 92 percent of all stems and 91 percent of all tree sites sampled were infected, and 22 percent of all tree sites were dead from WPBR.

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